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THE DIFFICULTIES IN THE HEREDITY THEORY.

By Henry Fairfield Osborn.

The Cartwright Lectures for 1892, II.

(*Continued from Page 481, Vol. XXVI.*)

"Nur muss ich nochmals betonen, dass nach meiner Auffassung der Anfang einer neuen Reihe erblicher Abweichungen, also auch der Eintritt einer neuen Art ohne eine vorausgegangene erworbene Abweichung undenkbar ist."—Virchow.

State of Opinion.—The above quotation from one of the most eminent authorities of our times represents the unshaken conviction of a very large class upon one side of the question of transmission of acquired characters, which is met by equally firm conviction upon the other side.

Herbert Spencer, whose entire system of biology, psychology, and ethics is based upon such transmission, says: "I will only add that, considering the width and depth of the effects which acceptance of one or other of these hypotheses must have on our views of Life, Mind, Morals, and Politics, the question Which of them is true? demands, beyond all other questions whatever, the attention of scientific men."[1] This shows that Spencer considers the matter still *sub judice*, and lest you may think I am bringing before you an issue in which learning and experience are ranged against ignorance and prejudice, I have taken some pains, by correspondence

[1]Nineteenth Century, 1889.

with a number of friends abroad, to learn the present state of opinion. The two leading English and French authorities upon this subject express themselves doubtfully.

Galton's mind is still wavering, as in his work of 1889:[1] "I am unprepared to say more than a few words on the obscure, unsettled and much discussed subject of the possibility of transmitting acquired faculties. . . . There is very little direct evidence of its influence in the course of a single generation, if the phrase of Acquired Faculties is used in perfect strictness and all inheritance is excluded that could be referred to some form of Natural Selection, or of Infection before birth, or of peculiarities of Nurture and Rearing."

Ribot, although in the center of the French Lamarckians, says: "Notwithstanding these facts the transmission of acquired modifications appears to be very limited, even when occurring in both of the parents."

Excepting from Kölliker; His, the Leipzig anatomist; Pflüger, the physiologist; Ziegler, in pathology; and De Vries, in botany, Weismann has not found much sympathy from his own countrymen in his opinion "that acquired characters cannot be transmitted; . . . that there are no proofs of such transmission, that its occurrence is theoretically improbable, and that we must attempt to explain the transformation of species without its aid."[2] Besides Virchow[3] and Eimer,[4] Haeckel has expressed himself strongly against Weismann. My colleague, Professor Wilson, writes me (Munich, December 31, 1891) that, while Weismann's modified theories as to the phenomena in the productive cells are pretty generally accepted, Hertwig, Hofer, Paully, Boveri, and others are pronounced advocates of the acquired-character-transmission theory.

In Paris, Brown-Séquard, who was among the first to test this problem experimentally by observing the inheritance of the effects of nerve-lesions; his assistant Dupuy, Giard, Duval,

[1]Natural Inheritance, 1889, p. 14.

[2]Biologisches Centralblatt, 1888, pp. 65 and 97.

[3]Ueber den Transformismus, Archiv. f. Anthropologie, 1889, p. 1.

[4]Organic Evolution, upon the Law of Inheritance of Acquired Characters. Tübingen, 1888. Trans.

Blanchard, and others are on the affirmative, or Lamarckian side.

Physiologists generally have fought shy of the question, although I think in the end they will be forced to take it up with the morphologists, and give us the physio-morphological theory of heredity of the future. Professor Michael Foster of Cambridge, and Professor Burdon-Sanderson, of Oxford, both write me that the question has hardly come into the physiological stage of inquiry at all. Yet in England Weismann has found his strongest supporters among some of the naturalists: Wallace, Lankester, Thiselton Dyer, Meldola, Poulton, Howes, and others; while, excepting Windle, the anatomists, including Mivart and Lawson Tait, with Sir William Turner as the most prominent, are all Lamarckians. Huxley, Romanes, and Flower are said to be doubtful. In this country the opinion of naturalists is directly the outgrowth of the class of studies in which each happens to be engaged. So far as I know every vertebrate and invertebrate palæontologist is a Lamarckian,[1] for in this field all evolution seems to follow the lines of inherited use and disuse; most of those engaged upon invertebrate zoology incline to follow Weismann. I have conversed upon this subject with many physicians, and find that without exception the transmission of acquired characters is an accepted fact among the profession.

Exact Statement of the Problem.—It is important at the outset to state most clearly what is and what is not involved in this discussion. Weismann[2] does not claim that the reproductive or germ-cells are uninfluenced by habit; on the other hand, he admits that most important modifications in these cells may and do result from changes of food, climate, from healthy or unhealthy conditions of the body; also from infectious disease, where it is quite as possible that the microbes may enter the reproductive cells as any other cells of the body; from alcoholism, where the normal molecular action of the protoplasm of the germ-cells may be disturbed,

[1]See the writings of Hyatt, Cope, Ryder, Dall, Scott, and others.

[2]See Essays upon Heredity and Kindred Biological Problems, 1889. Trans.

resulting in abnormal development, and there are some very interesting experiments which I shall cite on this point; from some nervous disorders which profoundly modify cell-function in all the tissues; in other words, *ovum sanum in corpore sano.* But to accept all this, and even to include all our rapidly increasing knowledge of the direct relation between such phenomena as production of deformities and determination of sex, and the influences of environment upon the ovum; or the influences of the mother upon the fœtus—this is all aside from the real question at issue.

It may be stated thus: Given *G*, the ova and spermatozoa, the germ-cells or material vehicles of hereditary characters; *S*, the body of somatic cells of all the other tissues conveying the hereditary characters of nerve, muscle, and bone; *V*, the variations in these body-cells "acquired" during lifetime; given these factors, the real question is: Do influences at work producing variations in certain body-cells of the parent so affect the germ-cells of the parent that they reappear in corresponding body-cells of the offspring? To take a concrete case, will the increased use of the cells of the extensor indicis muscle in the parent so stimulate that portion of the germ-cells which represents this muscle that the increment of growth will in any degree reappear in the offspring?

This is what is required of heredity upon the Lamarckian hypothesis, and I think you will see at once that while this hypothesis simplifies the problem of evolution it in a corresponding degree renders more difficult the problem of heredity —for we have not the first ray of knowledge of what such a process involves. There is no quality more essential to the scientific progress than common honesty; if we take a position let us face all its consequences; the more we reflect upon it, the more serious the Lamarckian position becomes.

In the present lecture let us first briefly review the progress of the science of heredity which has led up to the present discussion. Second, Let us examine the evidence for and against the Lamarckian theory, and inquire how far natural selection can explain all the facts of evolution. Third, Let us examine the evidence for such a continuous relation between

the body-cells and the germ-cells, as must exist if the Lamarckian theory is the true one.

History of the Heredity Theory.—In a valuable summary of the past theories of heredity[1] J. A. Thomson distinguishes three general problems, which are often confused. 1st. What characters distinguish the germ-cells from other cells of the body? 2d. How do the germ-cells derive these distinguishing characters? 3d. How shall we interpret "particulate" inheritance, or the reappearance of single peculiarities in the offspring?

The various theories may be grouped under two heads, "Pangenesis of Germ-cells" and "Continuity of Germ-cells," according to the dominating idea in each.

1. *Pangenesis.*—The idea prevading pangenesis was first expressed by Democritus that the "seed" of animals was derived by contributions of material particles from all parts of the bodies of both sexes, and that like parts produced like. Two thousand years later, Buffon revived this conception of heredity in his "molecules organiques." In 1864 Herbert Spencer suggested the existence of "physiological units," derived from the body-cells of the parent, forming the germ-cells and then developing into the body-cells of the offspring.

It is interesting to note the course of Darwin's thought upon this matter in his published works and in his "Life and Letters." He was at first strongly opposed to the views upon evolution advanced by Buffon, by Erasmus Darwin, his grandfather, expanded by Lamarck, and now known as Lamarckian. But gradually becoming convinced that his own theory of natural selection could not account for all the facts of evolution, he unconsciously became a strong advocate of Lamarck's theory, and contributed to it a feature which Lamarck had entirely omitted, namely, a theory of heredity expressly designed to explain the transmission of acquired characters. Darwin's[2] "provisional hypothesis of pangenesis" postulated a material connection between the body-cells and

[1]See Proc. Roy. Soc. Edin., 1888, p. 93.

[2]See Animals and Plants under Domestication, 1875, vol. ii., p. 349.

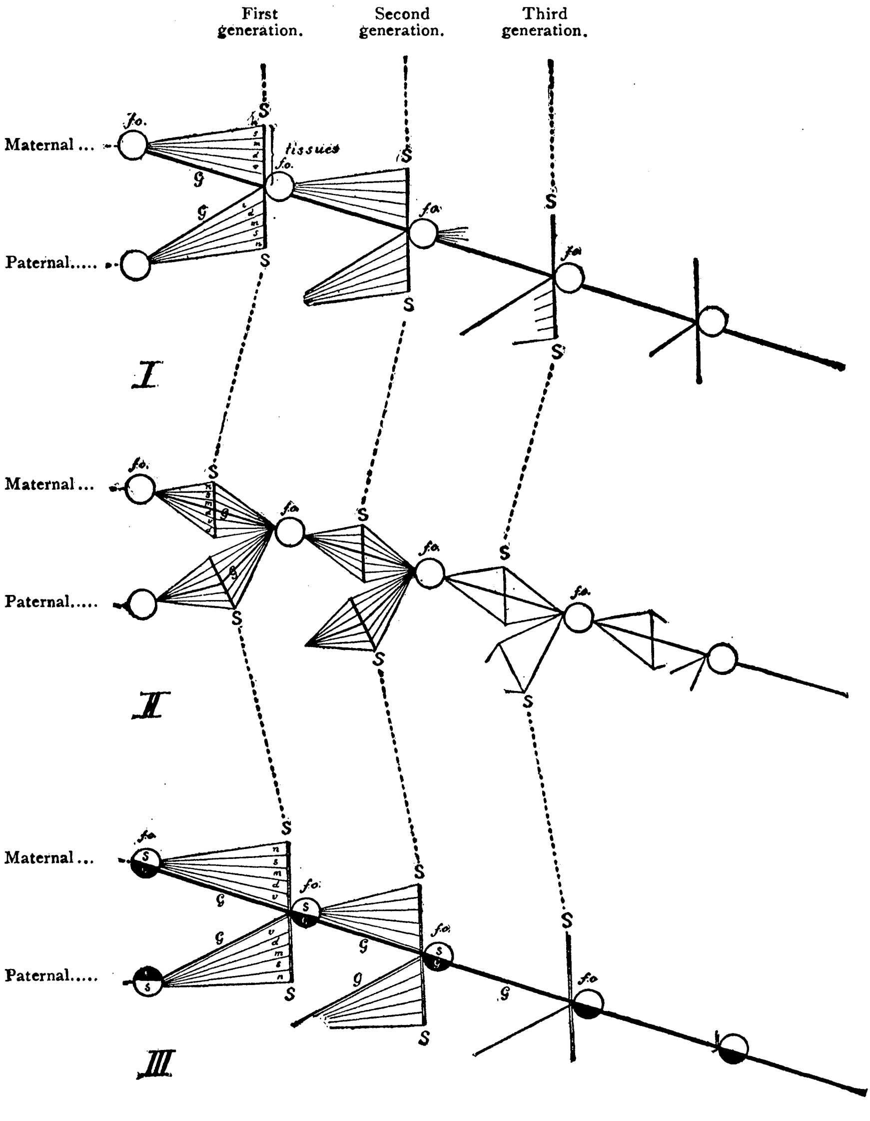
the germ-cells by the circulation of minute buds from each cell; each body-cell throws off a "gemmule" containing its characteristics; these gemmules multiply and become especially concentrated in the germ-cells; in the latter they unite with others like themselves; in course of development they grow into cells like those from which they were originally given off. (See Diagram II.)

Galton,[1] who has always been doubtful in regard to use-inheritance, while advancing a theory of "continuity," partly approved Darwin's pangenesis idea in the cautious statement: "Each cell may throw off a few germs that find their way into the circulation and thereby have a chance of entering the germ-cells." At the same time Galton contributed very important experimental disproof of the existence of "gemmules," and, in fact, of the popular idea, of the circulation of hereditary characters in the blood, by a series of careful experiments upon the transfusion of blood in rabbits; he found that the blood did not convey with it even the slightest tendency to transfer normal characteristics from one variety to another.

Professor Brooks,[2] of the Johns Hopkins University, then contributed an original modification of pangenesis in which the functions of the ova and spermatozoa were sharply differentiated. (1) He regarded the ovum as a cell especially designed as a storehouse of hereditary characteristics, each characteristic being represented by material particles of some kind; thus hereditary characters were handed down by simple cell division, each fertilized ovum giving rise to the body-cells in which its hereditary characters were manifested and to new ova in which these characters were conserved for the next generation (this portion of Brooks's theory is very similar to Galton's and Weismann's). 2. The body-cells have the power of throwing off "gemmules," but this is exercised mainly or exclusively when its normal functions are disturbed, as in metatrophic exercise or under change of environment. 3. These gemmules may enter the ovum, but the spermatozoan is their main center. According to this view the female

[1]Contemporary Review, vol. xxvii., p. 80–95.

[2]The Law of Heredity, 1883.



f. o., fertilized ovum or *embryo*, containing maternal and paternal characteristics; *S*, soma, or adult body, containing *n, s, m, d, v*, *somatic cells* of the various tissues; and *G*, *germ-cells* of the reproductive glands.

I. HISTOGENESIS.—Showing the successive rise *G*, and union *f. o.* of the maternal and paternal germ-cells by direct histogenesis.

II. PANGENESIS.—Showing the tissues of the body *S*, contributing to the germ-cells *G*, so that each *f. o.* is composed of elements from both the somatic and germ-cells.

III. CONTINUITY.—Showing the division of the embryo, *f. o.*, into somatoplasm, *s* (from which arise the body-cells), and germ-plasm, *G* (which passes direct to the germ-cells), establishing a direct continuity.

cell is rather conservative and the male cell progressive; the union of these cells produces variability in the offspring, exhibited especially in the regions of the offspring corresponding to the regions of functional disturbance in the parent. This hypothesis was well considered, and while that feature of it which distinguishes the male and female germ-cells as different in kind has been disproved, and the whole conception of gemmules is now abandoned, the fact still remains that we shall nevertheless be obliged to offer some hypothesis to explain the facts disregarded by Weismann for which Brooks provides in his theory of the causes of variation.

2. *Continuity of Germ-cells.*—The central idea here is an outgrowth of our more modern knowledge of embryogenesis and histogenesis, and is, therefore, comparatively recent; it is that of a fundamental distinction between the "germ-cells," as continuous and belonging to the race, and the "body-cells," as belonging to the individual. Weismann has refined and elaborated this idea, but it was not original with him.

Richard Owen,[1] in 1849, Haeckel,[2] in 1866, Rauber,[3] in 1879, in turn dwelt upon the distinction which Dr. Jaeger, now of manufacturing fame, first clearly stated:

"Through a great series of generations the germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic portion, out of which the individual is built up, and a phylogenetic portion, which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as the continuity of the germ protoplasm. . . . Encapsuled in the ontogenetic material the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters." The latter idea has, under Weismann, been expanded into the theory of isolation of the germ-cells.

Galton introduced the term "stirp" to express the sum total of hereditary organic units contained in the fertilized ovum. His conception of heredity was derived from the

[1]See Parthenogenesis, in his Anatomy of Vertebrates.

[2]Generelle Morphologie, vol. ii., p. 170.

[3]Zool. Anz., vol. ix., p. 166.

study of man, and he supported the idea of continuity in the germ-cells in order to account for the law of transmission of "latent" characters; it is evident from this law that only a part of the organic units of the "stirp" become "patent" in the individual body; some are retained latent in the germ-cells, and become patent only in the next or some succeeding generation. For example, the genius for natural science was "patent" in Erasmus Darwin, grandfather of the great naturalist, it was "latent" in his son, and reappeared intensified in his grandson, Charles Darwin. I have elsewhere[1] summed up as follows Galton's general results, which so remarkably strengthen the "continuity" idea: We are made up, bit by bit, of inherited structures, like a new building, composed of fragments of an old one, one element from this progenitor, another from that, although such elements are usually transmitted in groups. The hereditary congenital constitution thus made up is far stronger than the influences of environment and habit upon it. A large portion of our heritage is unused, for we transmit peculiarities we ourselves do not exhibit. The contributions from each ancestor can be estimated in numerical proportions, which have been exactly determined, from statistics of stature in the English race; thus the contributions from the "patent" stature of the two parents together constitute one-half; while the contributions by "latent" heritage from the grandparents constitute one-sixteenth, etc. One of the most important demonstrations by Galton, is the *law of regression;* this is the factor of stability in race type which acts as gravitation does upon the pendulum; if an individual or a family swing far from the average characteristics of their race, and display exceptional physical or mental qualities, the principle of regression in heredity tends to draw their offspring back to the average.

Now how shall we distinguish regression from reversion? Very clearly, I think; *regression* is the short pull which tends to draw every variation and the individual as a whole back to the contemporary typical form, while *reversion* is the long pull which draws the typical form of one generation back to

[1]Atlantic Monthly, March, 1891, p. 359.

the typical form of a very much earlier generation. These forces are evidently akin, and in the shades of transition from one type to another we would undoubtly find a constant diminution numerically in the recurrence of characters of the older type, and thus "regression" would pass insensibly into "reversion."

Weismann has carried the idea of continuity to its extreme in his simple and beautiful theory of heredity, which is founded upon the postulate that there is a distinct form of protoplasm, with definite chemical and molecular properties, set apart as the vehicle of inheritance; this is the *germ-plasm*, *G*, quite separate from the protoplasm of the body-cells or *somatoplasm*, *S.* Congenital characters arising in the germ-cells are called *blastogenetic*, while acquired characters arising in the body-cells are *somatogenetic.*

To clearly understand this view, let us follow the history of the fertilized ovum in the formation of the embryo. It first divides into somatoplasm and germ-plasm (see Diagram III.), the former supplies all the tissues of the body—*n*, *s*, *m*, *d*, *v*, nervous, muscular, vascular, digestive, etc.—with their quota of hereditary structure; the residual germ-plasm is kept distinct throughout the early process of embryonic cell division until it enters into the formation of the nuclei of the reproductive cells, the ova or spermatozoa. Here it is isolated from changes of function in the somatoplasm, and in common with all other protoplasm is capable of unlimited growth by cell division without loss or deterioration of its past store of hereditary properties; these properties are lodged in the nucleus of each ovum and spermatozoan, and these two cells, although widely different in external accessory structure (because they have to play an active and passive part in the act of conjugation), are exactly the same in their essential molecular structure, and the ancestral characters they convey differ only because they come along two different lines of descent. When these cells unite they carry the germ-plasm into the body of another individual. Thus the somatoplasm of each individual dies, while the germ-plasm is immortal; it simply shifts its abode from one generation to another; it constitutes the

chain from which the individuals are mere offshoots. Thus the germ-plasm of man is continuous with that of all ancestors, in his line of descent, and we have an explanation of the early stages observed in development in which the human embryo passes through a succession of metamorphoses resembling the adult forms of lower types.

In order to emphasize, as it were, the passage of the germ-plasm from one generation to another without deterioration in its marvellous hereditary powers, Weismann added the idea of its *isolation.* Not only does he repudiate the pangenesis notion of increment of germ-plasm by addition of gemmules, but he believes that it is unaffected by any of the normal changes in the somatic or body-cells. As this continuity and isolation would render impossible the transmission of characters acquired by the somatoplasm, Weismann began to examine the evidence for such transmission, and coming to the conclusion that it was insufficient, in his notable essay on "Heredity," in 1883, he boldly attacked the whole Lamarckian theory and has continued to do so in all his subsequent essays.

Being forced to explain evolution without this factor, he claimed that variation in the germ-plasm was constantly arising by the union of plasmata from different lines of descent in fertilization, and that these variations are constantly being acted upon by Natural Selection to produce new types. He thus revived Darwin's earlier views of evolution, and this in part explains his strong support by English naturalists.

It will be seen at once that there are a number of distinct questions involved.

The matter of first importance in life is *the repetition and preservation of type,* the principle which insures the unerring accuracy and precision with which complex organs are built up from the germ-cells; the force of regression and the more remote forces of reversion all work in this conservative direction; the theory of the preservation of these forces in a specific and continous form of protoplasm is by far the most plausible we can offer at present. The matter of second importance, but equally vital to the preservation of races, in the long run, is *the formation of new types* adapted to new circumstances of

life. I shall now attempt to show that the facts of evolution, while not inconsistent with the idea of continuity of the germ-plasm, are wholly at variance with the idea of its independence, separation, or isolation from the functions of the body. This can be done by proving, first, that the theory of evolution solely by natural selection of chance favorable variations in the germ-plasm is inadequate; second, that the inheritance of definite changes in the somatic cells is also necessary to evolution, and therefore there must exist some form of force or matter which connects the activities of the somatoplasm with those of the germ-plasm.

In the following table are placed some of the facts of human evolution which we have observed in the first lecture, and as they are part of inheritance, they also constitute the main external phenomena of heredity:

Phenomena of Heredity.

Conservative (toward past type).	*Neutral.*	*Progressive* (toward future type).
a. Repetition of parental type.	Fortuitous	*a.* Definite Variation in single characters, by accumulation=.
	and	
b. Regression (in many characters) to contemporary race type.	Indefinite	*b.* Definite Variation in many characters (from contemporary race type).
c. Reversion (mainly in single characters) to past race type.	Variations.	

What are the causes of these various phenomena?

Factors of Evolution.—The term "kinetogenesis" has been applied to the modern form of the Lamarckian theory, for it is an application of kinetic or mechanical principles to the origin of all structures such as teeth, bone, and muscle. It would be fatal to this theory, if it could be shown that the

changes taking place in course of a normal individual life, under the laws of use and disuse, are inadaptive, or do not correspond to those observed in the evolution of the race.

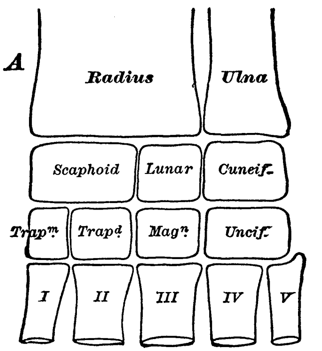
The Relative Growth of Organs.—Ball,[1] in his long argument against Lamarckianism, claims that such is the case, and that use-inheritance would be an actual evil: "Bones would often be modified disastrously. Thus the condyle of the human jaw would become larger than the body of the jaw, because as the fulcrum of the lever it receives more pressure. Some organs (like the heart, which is always at work) would become inconveniently or unnecessarily large. Other absolutely indispensible organs which are comparatively passive or are very seldom used would dwindle until their weakness caused the ruin of the individual or the extinction of the species." He later cites from Darwin[2] the "Report of the United States Commission upon the Soldiers and Sailors of the Late War," that the longer legs and shorter arms of the sailors are the reverse of what should result from the decreased use of the legs in walking and increased use of the arms in pulling. A little reflection on Mr. Ball's part would have spared us this crude exception, for whatever difficulties may arise from theoretical speculation as to the laws of growth, or from statistics, the fact remains that activity must increase adaptation in every part of the organism; otherwise the runner and the trotting horse should be kept off the track to increase their speed, the pianist should employ as little finger-exercise as possible. If the growth tendencies in single organs are transmitted, it is evident that the adaptive adjustments between these tendencies will also be transmitted.

The Feet.—In point of mechanical adaptation, man, with the single exception of his thumb and forearm, has not progressed beyond the most primitive eocene quadruped. The laws of evolution of the foot in the ungulate or hoofed animals, which have been especially studied by Kowalevsky, Ryder, Cope, and myself, afford a conclusive demonstration that the skeletal changes in the individual coincide with those which

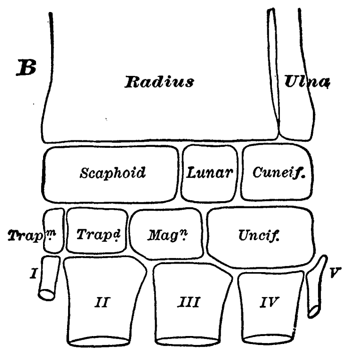
[1] Op. cit., p. 129.

[2] Descent of Man, p. 32.

will mark the evolution of the race. In the earliest ungulates the carpals and tarsals are disposed, as in man, directly above each other, with serial joints, as in *A*; in the course of evolution all these joints became interlocking, as in *B*, thus producing an alternation of joints and surfaces similar to those which give strength to masonry. In studying these facts Cope[1] reached a certain theory as to the motion of the foot and leg in locomotion. In trying to apply this, I found it could not be harmonized with all the facts, and I worked out an entirely different theory.[2] This I found subsequently coincided exactly with the results previously obtained by Muybridge, by the aid of instantaneous photographs, and summarized by Professor Harrison Allen, of the University of Pennsylvania.[3]



PRIMITIVE UNGULATE FOOT.—Lines of vertical cleavage on either side of the middle toe, III. Spreading of toes would cause separation of the carpals.



RECENT UNGULATE FOOT.—No lines of verticle cleavage. All joints broken by enlargement of scaphoid, unciform, and radius, the bones receiving greatest impact in walking. Lateral toes, I., V., degenerate.

The monodactylism of the horse was attained by the atrophy of the lateral toes, and concentration of the major axis of body-weight and strain upon the middle finger and toe. Man is also tending toward monodactylism in the foot

[1]AMERICAN NATURALIST, 1887, p. 986.

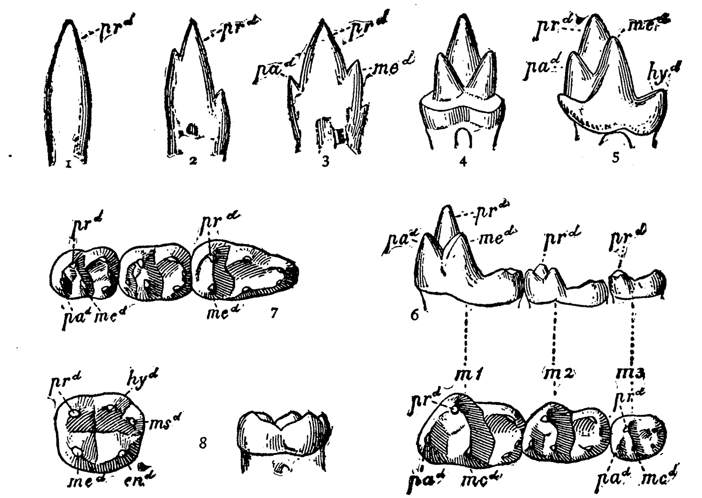
[2]See Trans. of American Philosophical Society, p. 561. Philadelphia, 1889.

[3]The Muybridge Work at the University of Pennsylvania. Philadelphia, 1888.

by the establishment of the major axis through the large toe and atrophy of the outer toes. The present atrophy of our small toe is as good a parallel as we can find of the changes which were occurring in the eocene period among the ancestors of the horse.

The Teeth.—But how about the teeth, in which there is an absolute loss of tissue in consequence of use? This is another objection raised by Ball, Poulton, and others which disappears upon examination.

The dental tissues, while the hardest in the body, and, unlike bone, incapable of self-repair, are not only both living and sensitive, but, to a very limited degree, plastic and capa-

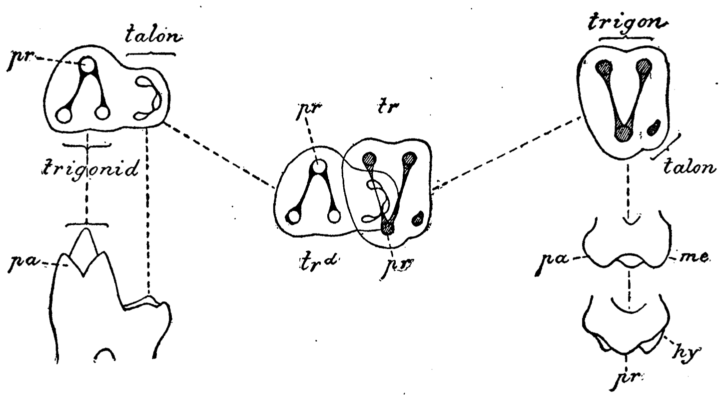


EVOLUTION OF THE CUSPS OF THE HUMAN LOWER MOLAR.—*prd*, protoconid (anterior buccal cusp); *pad*, paraconid; *med*, metaconid (anterior lingual cusp); *hyd*, hypoconid (posterior buccal); *end*, entoconid (posterior lingual cusp); *msd*, mesoconulid (intermediate cusp). Fig. 1.—Reptilian stage. Fig. 2-5.—Mesozoic mammals, first lower molars showing rise of ancestral cusps. Fig. 6.—Eocene carnivore (*Miacis*), showing how the low tubercular crown *m3* is derived from the high crown *m1*. Fig. 7.—Eocene monkey (*Anaptomorphus*), showing how the primitive anterior lingual cusp, *pad*, disappears. Fig. 8.—Human first molar with its ancestral cusps.

ble of change of form. *Ex hypothesi*, it is not the growth, but the reaction tendency which produces the growth, which is transmitted. The evolution of the teeth, therefore, falls into the same category as bone.[1] In the accompanying figures I

[1]See especially the papers of Ryder, Cope, and the writer, "Evolution of Mammalian Molars to and from the Tritubercular Type," American Naturalist, 1889.

have epitomized the slow transformation of the single-fanged conical reptilian tooth, such as we see in the serpents, into the low-crowned human grinder. We now know all the transition forms, so that we can homologize each of the cusps of the human molar with its varied ancestral forms in the line of descent. For example, the anterior lingual or inner cusp of the upper true molars traces its pedigree back to the reptilian cone. The anterior triangle of cusps, or trigon, seen in the mosozoic mammalia, and persisting in the first inferior true molar of the modern dog, is still seen in the main portion of the crown of the human upper molars (*pr*, *pa*, *me*). To this was added, ages ago, the posterior lingual cusp, or hypocone, which, as Cope has shown, is exhibited in various degrees of development in different races and is an important race



Lower molar. Upper and lower molars opposed. Upper molar.

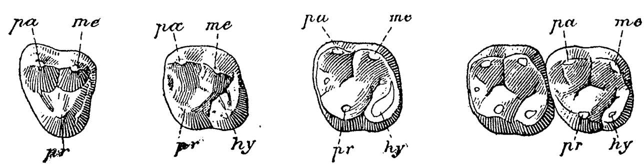
KEY TO PLAN OF UPPER AND LOWER MOLARS IN ALL MAMMALS.—Each tooth consists of a triangle, *trigon*, with the protocone, *pr*, at the apex. The apex is on the inner side of the upper molars and on the outer side of the lower molars.

index.[1] A glance through the diagrams shows that the development of the crown has been by the successive addition of new cusps. Without entering upon the details of evidence which would be out of place here, I may say briefly that the new main cusps have developed at the points of maximum

[1]The upper molars in many Esquimaux are triangular (as in Fig. 11); in most negroes they are square (Fig. 12). In our race they are intermediate.

wear (*i. e.*, use), and conversely in the degeneration of the crown, disuse foreshadows atrophy and disappearance.

Upon the whole, with some exceptions which we do not at present understand, the course of evolution of the teeth supports the evidence derived from the skeleton, that, whether any true causal relation has existed or not, the lines of individual transformation in the whole fossil series preceded those of race transformation.



9 10 11 12

EVOLUTION OF THE HUMAN UPPER MOLARS.—Fig. 9.—*Anaptomorphus*, a lower eocene monkey. Fig. 10.—An upper eocene monkey. Fig. 11 and 12.—Human, 11, Esquimaux; 12, negro. See addition of "talon," *hy*, to "trigon" composed of *pa*, *pr*, *me*.

The Rise of New Organs.—We owe to Dr. Arbuthnot Lane a most interesting series of studies upon the influences of various occupations upon the human body. He proves conclusively that individual adaptation not only produces profound modifications in the proportions of the various parts, but gives rise to entirely new structures.

His anatomy and physiology of a shoemaker[1] shows that the lifelong habits of this laborious trade produce a distinct type, which if examined by any zoological standard would be unhesitatingly pronounced a new species—*homo sartorius.* The psychological analysis which a Dickens or Balzac would draw, showing the influences of the struggle for existence upon the spirit of this little tailor could not be more pathetic than Dr. Lane's analysis of his body. The bent form, the crossed legs, thumb and forefinger action, and peculiar jerk of the head while drawing the thread, are the main features of sartorial habit. The following are only a few of the results: The muscles tended to recede into tendons and the bony surfaces into which they were inserted tended to grow in the

[1]Journal of Anatomy and Physiology, 1888, p. 595.

direction of the traction which the muscle exerted upon them. The articulation between the sternum and the clavicle was converted into a very complex arthrodial joint, constituting almost a ginglymoid articulation. The sixth pair of ribs were anchylosed to the bodies of the vertebræ, indicating that they had ceased to rise and fall with sternal breathing, and that respiration was almost exclusively diaphragmatic. The region of the head and first two vertebræ of the neck was still more striking: the transverse process of the right side of the atlas, toward which the head was bent, formed a new articulation with the under-surface of the jugular process of the occipital bone, "a small synovial cavity surrounded this acquired articulation, but there was no appearance of a capsular ligament;" the left half of the axis was united by bone to the corresponding portion of the third cervical; there was found a new upward prolongation of the odontoid peg of the axis, and a new accessory transverse ligament to keep it from pressing upon the cord. In short, "the anatomy of the shoemaker represents the fixation and subsequent exaggeration of the position and tendencies to change which were present in his body when he assumed the position for a short period of time.

Rate of Inheritance.—This illustration serves also to emphasize the great contrast between the rapidity of individual transformation and the slowness of race transformation. No one would expect the son of this shoemaker to exhibit any of these acquired malformations. Yet Dr. Lane thinks he has observed such effects in the third generation by the summation of similar influences.

All palæontological evidence goes to show that the effects of normal habits, if transmitted at all, would be entirely imperceptible in one generation. The horse, for example, has not yet completely lost the lateral toes which became useless at the end of the upper eocene period. This objection as to rate of evolution may be urged with equal force against the natural-selection theory. It is obvious that the active progressive principle in evolution, whatever it is, must contend with the enormous conservative power of inheritance, and

this, to my mind, is one of the strongest arguments against the possibilities of the rise of adaptive organs by the selection of chance favorable variations in the germ-plasm.

Application to Human Evolution.—Principles underlying these illustrations may now be applied to some of the facts in human evolution brought out in the first lecture. They show that if functional tendencies are transmitted we can comprehend the distinct evolution history of each organ; the rise and fall of two organs side by side; the definite and purposive character of some anomalies; the increase of variability in the regions of most rapid evolution; the correlation of development, balance and degeneration in the separate organs of the shoulder, hand and foot.

Yet even granting this theory, there still remain difficulties. The relation of use and disuse to some of the contemporary changes in the human backbone is rather obscure. I would hesitate to pronounce an opinion as to whether our present habits of life are tending to shorten the lumbars, increase the spinal curvatures, and shift the pelvis, without making an exhaustive study of human motion. Among the influences which Dr. Lane has suggested[1] as operative here are the wearing of heeled shoes and the increase of the cranium. He considers the additional or 6th lumbar vertebra as a new element rather than as a reversion, and works out in some detail the mechanical effects of the presence of the fœtus upon female respiration (*i.e.*, in the sternal region) and upon the pelvis. Now, if it be true that the female pelvis is relatively larger in the higher races than in the lower, I do not think that Dr. Lane can sustain his point, because in the lower races the fœtus is carried for an equally long period, during a much more active life, and in a more continuously erect position. Therefore, if these mechanical principles were operating, the pelvis in the modern lower races should be larger than in the higher. On the other hand, the form of the female pelvis in the higher races is one of the best established selecting or eliminating factors, a large pelvis favoring frequent births

[1]Journal of Anatomy and Physiology, 1888, p. 219.

and the preservation of those family stirps in which it occurs. I mention this to show how cautious we must be in jumping to conclusions as to kinetogenesis.

The transformism in all the external features of the skull, jaws, and teeth may be attributed to inherited tendencies toward hypertrophy or atrophy; but how about the convolutions of the turbinal bones or the complex development of the semicircular canals and cochlea of the internal ear and the many centers of evolution which are beyond the influences of use and disuse? These are examples of structures which fortify Weismann's contention, for if complex organs of this character can only be accounted for by natural selection, why consider selection inadequate to account for all the changes in the body?

Difficulties in the Natural-Selection Theory.—The answer, I think, is readily given: We do not know whether use and disuse are operating upon the mechanical construction of the ear; we do know that the organ can be rendered far more acute by exercise; but even if it were true that habit can exert no formative influence, the ear is one of those structures which since its first origin has been an important factor in survival, and *may* therefore have been evolved by natural selection. Now the very fact that selection may have to care for variations in such prime factors in survival as the ear, renders it the more difficult to conceive that it also is nursing the minutiæ of variation in remote, obscure, and uncorrelated organs.

Even in the brief review of human evolution in the first lecture I have pointed out eight independent regions of evolution, upward of twenty developing organs, upward of thirty degenerating organs. A more exhaustive analysis would increase this list tenfold. Now, where chance variation should produce an increase in size in all the developing organs, and a decrease in size of all the degenerating organs, and an average size in all the static organs, we would have all the conditions favoring survival. But the chances are infinity to one against such a combination occurring unless the tendencies of variation are regulated and determined, as

Lamarckians suppose, by the inheritance of individual tendencies. But may not the favorable variations in the body be grouped to either outweigh or underweigh the unfavorable variations? This would be possible if combinations occurred, but we can readily see that combinations, such as we observe in the separate elements in the foot alone, completely neutralize each other so far as "survival" is concerned; how the foot would neutralize the hand, or the foot and hand would neutralize the lumbar region.[1]

It is this consideration of single organs, the observation of their independent history, the rise of new compound organs, by steady growth from infinitesimal beginnings of their separate elements, the combined testimony of anatomy and palæontology which force us to regard the theory of evolution by the natural selection of chance variations as wholly untenable. With the utmost desire to regard the discussion in as fair a spirit as possible, the explanations offered by the adherents of Weismann's doctrine strike me as strained, evasive, and illogical.[2]

We can, however, by no means undervalue or dispense with natural selection, which must be in continuous operation upon every character of sufficient importance to weigh in the scale of survival. I need hardly remind you that this selecting principle was first discovered in 1813 by Dr. W. C. Wells, of Charleston, in connection with the immunity from certain tropical diseases enjoyed by negroes and mulattoes.[3]

The eliminating factor in selection is illustrated almost daily in cases of appendicitis. I regret I have not had time to ascertain whether or not this disease is considered due purely to accident or to congenital variation in the aperture of the appendix, which favors the admission of hard objects. If so, modern surgery is only benefiting the individual to the detriment of the race by its efficient preventive operations;

[1]I have expanded this idea fully in recent papers upon the theory of evolution of the horse. See "Are Acquired Variations Inherited?" AMERICAN NATURALIST, February, 1891.

[2]See Weismann's last essay, Retrogressive Development in Nature, Biol. Mem., trans., in press.

[3]See Introduction of Darwin's Origin of Species.

and every individual who succumbs to this disease can reflect with melancholy satisfation that he does so *pro bono publico.*

Conclusions as to the Factors of Evolution.—The conclusions we reach from the study of the muscular and skeletal systems are therefore as follows: 1st. That individual transformism in the body is the main determinant of variations in the germ-cells, and is therefore the main cause of definite progressive or retrogressive variations in single organs. 2d. That evolution in these organs is hastened, where all members of the race are subject to the same individual transformism. The contrast between the rate of individual transformism and race transformism is due to the strong conservative forces of the germ-plasma. 3d. That evolution is most rapid where variations are of sufficient rank to become factors in survival. Then selection and use-inheritance unite forces, as active progressive principles opposing the conservative principle in the germ-plasma. 4th. That fortuitous and chance variations also arise from disturbances in the body or germ-cells; they may be perpetuated, or disappear in succeeding generations.

Applying these views to variation there should, theoretically, appear to be just those two distinct classes of anomalies in the human body which we have seen actually occurring. First, those in the path of evolution, arising from perfectly normal changes in the somatoplasm and germ-plasm. Second, those wholly unconnected with the course of evolution, arising fortuitously or from abnormal changes in the somatoplasm or germ-plasm; to this head may be attributed the whole scale of deformities. Thus transformism and de-formism should be kept distinct in our minds. Nevertheless the facts of de-formism contribute the strongest body of evidence which we can muster at present to prove that there does exist a relation between the somatoplasm and germ-plasm which renders transformism possible.

The Relations between the Somatoplasm and Germ-plasm.—We have seen reasons to take a middle ground as to the distinct specific nature of the body cells and germ cells, and this position is, I think, strengthened the more broadly

we extend our inquiry into all the fields of protoplasmic activity.

There are three questions before us.

1. What is the evidence that the germ-plasm and somatoplasm are distinct?

2. What is the specific nature of the germ-plasm?

3. What is the nature of the relations which exist between the two?

1. The *separation of the germ-plasm* is in the regular order of evolution upon the principles of physiological division of labor. The unicellular organisms combine all the functions of life in a single mass of protoplasm, that is, in one cell. In the rise of the multicellular organisms the various functions are distributed into groups of cells, which specialize in the perfecting of a single function. Thus the reproductive cells fall into the natural order of histogenesis, and the theory of their entire separation is more consistent with the laws governing the other tissues than the theory which we find ourselves obliged to adopt, that while separate they are still united by some unknown threads with the other cells.

The morphological separation of what we may call the race-protoplasm becomes more and more sharply defined in the ascending scale of organisms. Weismann's contention as to the absolutely distinct specific nature of the germ-plasm and somatoplasm has, however, to meet the apparently insuperable difficulty that in many multicellular organisms, even of a high order, the potential capacity of repeating complex hereditary characters, and even of producing perfect germ-cells, is widely distributed through the tissues.

For example, cuttings from the leaves of the well-known hot-house plant, the begonia, or portions of the stems of the common willow-trees, are capable of reproducing complete new individuals. This would indicate either that portions of the germ-plasm are distributed through the tissues of these organisms, or that each body-cell has retained its potential quota of hereditary characters.

Among the lower animals we find the same power; if we cut a hydra or bell-animalcule into a dozen pieces each may

reproduce a perfect new individual. As we ascend in the animal scale the power is confined to the reproduction of a lost part in the process known as recrescence. As you well know, in the group to which the frog and salamander belong, a limb or tail, or even a lower jaw may be reproduced. The only logical interpretation of these phenomena is that the hereditary powers are distributed in the entire protoplasm of the organism, and the capacity of reproduction is not exhausted in the original formation of the limb, but is capable of being repeated. There has been considerable discussion of late as to the seat of this power of *recrescence.* It seems to me not impossible that in the vertebrates it may be stored in the germ-cells, and it would be very interesting to ascertain experimentally whether removal of these cells would in any way limit or affect this power; we know that such removal in castration or ovariotomy sometimes profoundly modifies the entire nature of the organism, causing male characters to appear in the female, and female characters to develop in the male.

So far as man is concerned it has been claimed by surgeons that genuine recrescence sometimes occurs; for example, that a new head is formed upon the femur after exsection; but my friend Dr. V. P. Gibney informs me that this is an exaggeration, that there is no tendency to reproduce a true head, but that a pseudo-head is formed which may be explained upon the principle of regeneration and individual transformism by use of the limb.

Pflüger's opinion is that recrescence does not indicate a storage of hereditary power, that there is no pre-existing germ of the member, but that the re-growth is due to the organizing and distributing power of the cells at the exposed surface, so that as new formative matter arrives it is built up gradually into the limb. This view would reduce recrescence to the level of the *regeneration* process, which unites two cut sections of the elements of a limb in their former order. It is partly opposed to the facts above referred to, which seem to prove the distribution of the hereditary power. Yet it seems to me quite consistent to consider these three processes—*a*, reproduction of a new individual from every part; *b*, recrescence of a new

member from any part; *c*, regeneration of lost tissues—as three steps indicating the gradual but not entire withdrawal of the reproductive power into the germ-cells.

I have not space to consider all the grounds which support the view of the separation of the germ-cells in man. Some of the more prominent are the very early differentiation of these cells in the embryo, observed with a few exceptions in all the lower orders of animals, and advancing so rapidly in the human female that several months before birth the number of primordal ova is estimated at seventy thousand, and is not believed to be increased after the age of two and a half years. The most patent practical proof is that we may remove every portion of the body which is not essential to life and yet the power of complete reproduction of a new individual from the germ-cells is unimpaired. Among the many reasons advanced for pensioning the crippled soldiers of our late war you never hear it urged that their children are incapacitated by inheritance of injuries. The strongest proof, however, rests in the evidence I have already cited from heredity of the extraordinary stability of the germ-cells, which is the safeguard of the race.

2. The *specific nature of the germ-plasm* must be considered before we consider its relations. Wherein lies the conservative power of the germ-plasm, and in what direction shall we look for its transforming forces? You see at once that marvellous as is the growth of cells in other tissues, the growth of the germ-cell is still more so.

We find it utterly impossible to form any conception of the contents of the microcosmic nucleus of the human fertilized ovum, which is less than $\frac{1}{2500}$ of an inch in diameter, but which is, nevertheless, capable of producing hundreds of thousands of cells like itself, as well as all the unlike cells of the adult organism. We can only translate our ideas as to the possible contents of this nucleus in the terms of chemistry and physics.[1]

Spencer[2] assumed an order of molecules or units of proto-

[1]See Ray Lankester, Nature, July 15, 1876.

[2]Principles of Biology, vol. i, p. 256.

plasm lower in degree than the visible cell-units, to the internal or polar forces of which and their modification by external agencies and interaction, he ascribes the ultimate responsibility in reproduction, heredity and adaptation. This idea of biological units seems to me an essential part of any theory; it is embodied in Darwin's "gemmules," in Haeckel's "plastidules," yet, as Lankester says, the rapid accumulation of bulk is a theoretical difficulty in the material conception of units. In the direction of establishing some analogy between the repetition power of heredity and known function of protoplasm, Haeckel[1] and Hering[2] have likened heredity to memory, and advanced the hypothesis of persistence of certain undulatory movements; the undulations being susceptible of change and therefore of producing variability, while their tendency to persist in their established harmony is the basis of heredity. Berthold, Gautier and Geddes[3] have speculated in the elaboration of the idea of metabolism; the former holding the view that "inheritance is possible only upon the basis of the fundamental fact that in the chemical processes of the organism the same substances and mixtures of substances are reproduced in quantity and quality with regular periodicity."[4]

I have merely touched upon these speculations to show that the unknown factors in heredity are also the unknown factors in operation in living matter. All we can study is the external form and conjecture that this form represents matter arranged in a certain way by forces peculiar to the organism. These forces are exhibited or patent in the somatic cells; they are potential or latent in the germ-cells.

The last stage of our inquiry is as to the mode in which the action of habit or environment upon the somatic cells can be brought to bear upon the germ-cells.

[1]Perigenesis der Plastidule oder die Wellenzeugung der Lebenstheilchen. Jena, 1875.

[2]Ueber d. Gedächtniss als eine allgemeine Function d. organischen Materie. Vienna, 1870.

[3]See also Thomson, op. cit., p. 102.

[4]Berthold: Studien über Protoplasma-Mechanik. Leipzig, 1886.

The Nature of the Relation Between the Body-cells and Germ-cells.—I have already shown that we are forced to infer that such a relation exists by the facts of evolution, although these facts show that the transmission of normal tendencies from the body to the germ-cells is ordinarily an extremely slow process.

Virchow[1] says every variation in race character is to be traced back to the pathological condition of the originator. All that is pathological is not diseased, and inheritance of a variation is not from the influence upon one individual necessarily, but upon a row of individuals. This is in the normal condition of things. In the abnormal condition the rate of transmission may be accelerated.

Does this transmission depend upon an interchange of material particles or upon an interchange of forces, or both?

There are three phenomena about which there is much scepticism, to say the least, which bear upon the question of a possible interchange of forces between the body and germ-cells. These are the inheritance of mutilations, the influence of previous fertilization, and the influence of maternal impressions. They are all in the quasi-scientific realm, which embraces such mental phenomena as telepathy. That is, we incline to deny them simply because we cannot explain them.

Mutilations.—Since the publication of Weismann's essays the subject of inherited mutilations has attracted renewed interest. I would first call attention to the fact that this matter has only an indirect bearing, for a mutilation is something impressed upon the organism from without; it is not truly "acquired;" the loss of a part by accident produces a sudden but a less profound internal modification of the organism than the loss of a part by degeneration. Most of the results are negative; many of the so-called "certain" cases prove upon investigation to be mere coincidences. Weismann[2] himself experimented upon white mice, and showed that nine hundred and one young were produced by five generations of arti-

[1]Ueber den Transformismus, Archiv f. Anthropologie, 1888, p. 1.

[2]Biological Memoirs, p. 432.

ficially mutilated parents, and yet there was not a single example of a rudimentary tail or of any other abnormality in this organ. The cases of cleft ear lobule have recently been summed up.[1] Israel reports two cases of clefts in which the parent's ears were normal. Schmidt and Ornstein report affirmative cases. His shows that an affirmative case, cited by V. Zwieciki, is merely an inherited peculiarity. The entire evidence is unsatisfactory, and upon the whole is decidedly negative.

Not so, however, in cases where the mutilation results in a general disturbance of the normal functions of different organs, as in the experiments conducted by Brown-Séquard[2] upon guinea-pigs, in which we see "acquired variation" intensified. In these, abnormal degeneration of the toes, muscular atrophy of the thigh, epilepsy, exophthalmia, etc., appeared in the descendants of animals in which the spinal cord or sciatic nerve had been severed, or portions of the brain removed. It was also shown that the female is more apt to transmit morbid states than the male; that the inheritance of these injuries may pass over one generation and reappear in the second; that the transmission by heredity of these pathological results may continue for five or six generations, when the normal structure of the organs reappears. These cases, which are incontestable, at first sight appear to establish firmly the transmission of acquired characters; they were so regarded by Brown-Séquard. These lesions act directly upon the organs, and the abnormal growth in these organs appears to be transmitted. But can they not be interpreted in another way, namely, that the pathological condition of the nerve-centers has induced a direct disturbance in those portions of the germ-cells which represent and will develop into the corresponding organs of the future offspring?

Previous Fertilization.—Consider next the influence exerted upon the female germ-cell by the mere proximity of the male

[1] Journal of Anatomy and Physiology, 1891, p. 433.

[2] Comptes-Rendus, March 13, 1882. These experiments have been confirmed by Obersteiner.

germ-cell, as exhibited in the transmission of the characteristics of one sire to the offspring of a succeeding sire observed in animals, including the human species, also in plants. The best example is the oft-quoted case of Lord Morton's mare, which reproduced in the foal of a pure Arab sire the zebra markings of a previous quagga sire.

Some physiologists[1] have attempted to account for these remarkable indirect results from the previous fertilization or impregnation, by the imagination of the mother having been strongly affected or from interchange between the freely intercommunicating circulation of the embryo and mother, but the analogy from the action in plants (in which there is no gestation but early detachment and development of the fertilized cells) strongly supports the belief that the proximity of male germ-cells acts directly upon the female cells in the ovary. All that we can deduce from these facts is that in some manner the normal characteristics and tendencies of the ova are modified by the foreign male germ-cells without either contact or fertilization.

Maternal Impression.—The influence of maternal impressions in the causation of definite anomalies in the fœtus is largely a matter of individual opinion.

It is denied by some high authorities, led by Bergman and Leuckart.[2] Most practitioners, however, believe in it, and I need hardly add that it is a universal popular belief,[3] supported by numerous cases. I myself am a firm believer in it, from evidence which I am not free to publish. The bearing which the subject has upon this discussion is this: if a deviation in the development of a child is produced by maternal impression we have a proof that a deviation from normal hereditary tendencies can be produced without either direct vascular or nervous continuity.

We see an analogy between the experiments of Brown-Séquard, the influence of the previous sire, and the maternal

[1] See the cases cited by Ribot and Darwin: Animals and Plants under Domestication, vol. i, p. 437.

[2] Handwörterbuch der Physiologie, Wagner, Artikel "Zeugung," Leuckart.

[3] See Medical Record, October 31, 1891, an article by Joseph Drzewiecki, M. D.

influence. Neither, in my opinion, directly supports the theory of transmission of acquired characters, for they do not prove that normal changes in the body-cells directly react upon the germ-cells; they all show that the *typical hereditary development of single organs may be diverted by living forces which have no direct connection* with them according to our present knowledge.

What the nature of these forces is I will not undertake to say, but I believe we must admit the existence of some unknown force, or rather of some unknown relations between the body-cells and germ-cells.

A year ago, recognizing fully the difficulty of advancing any theory of heredity which would explain the transmission of acquired characters, I came to the following result: "It follows as an unprejudiced conclusion from our present evidence that upon Weismann's principle we can explain inheritance but not evolution, while with Lamarck's principle and Darwin's selection principle we can explain evolution, but not, at present, inheritance. Disprove Lamarck's principle and we must assume that there is some third factor in evolution of which we are now ignorant."

In this connection it is interesting to quote again from my colleague, Professor E. B. Wilson. He writes that the tendency in Germany at present is to turn from speculation to empiricism, and this is due partly "to the feeling that the recent wonderful advances in our knowledge of cell phenomena have enormously increased the difficulties of a purely mechanico-physical explanation of vital phenomena. In fact, it seems that the tendency is to turn back in the direction of the vital-force conception. . . . As Boveri said to me recently, 'Es gibt zu viel Vorstand in der Natur um eine rein mechanische Erklärung der Sache zu ermöglichen.'"

In the final lecture we turn to the forces exhibited in the germ-cells.

NOTE.—Bearing upon the experimental evidence for the hereditary transmission of multilations, I have recently received, through Dr. Charles E. Lockwood, of New York, a letter,[1] in regard to some experiments upon mice, which were continued over more generations than those of Weismann, and with affirmative results:

"I selected a pair of white mice on account of their rapid breeding. I bred them in and in for ninety six generations, as they breed every thirty days, and when they are thirty days old they are able to reproduce themselves. I destroyed all sickly and defective ones by breeding only the fittest. I bred all disease out of them, and had a pure-blooded animal, larger and finer every way than the original pair. In breeding their tails off, I selected a pair and put them in a cage by themselves, and when they had young I took the young and clipped their tails off. When old enough to breed I selected a pair from the young and bred them together, and when they had young I clipped their tails. I continued this breeding in and in, clipping each generation, and selecting a pair of the last young each time, in seven generations. Some of the young came without tails until I got a perfect breed of tailless mice. I then took one with a tail and one without a tail and bred them together, and by changing the sexes each time—a male without a tail, a female with a tail, and next a female without a tail, and a male with a tail—I was finally rewarded with all-tail mice."

There is such general scepticism now in regard to the inheritance of mutilations that it will be necessary to repeat such experiments as these in some well-known physiological laboratory. As told above, they seem to be trustworthy, but facts which go against a theory must be doubly attested.

[1]From A. J. S. Shiddell, Lexington, Ky.